

BIOGEOGRAPHICAL ASPECTS OF THE ANT FAUNA OF CORSICA (HYMENOPTERA: FORMICIDAE)

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Abstract.—Corsican myrmecofauna (26 genera, 83 species) is mostly European in characteristics and shows very low endemism (only 3 endemic species). A comparison with 15 neighboring countries shows its particular similarity with the faunas of Sardinia and Provence. Of the 83 species, 26 are widely distributed in most of these 15 countries. The origins of Corsican ant populations are discussed. The development of a modern fauna in Corsica before the island became isolated from the continent, human activity, distinctive conquering capacities of ants, their strong ability to settle in many habitats, interspecific competition and the great diversity of landscapes of the island explain the present composition of the myrmecofauna of Corsica.

Key Words.—Insecta, Corsica, Formicidae, biogeography, neighboring countries, competition.

Corsica is an island located in the western part of the Mediterranean, not far from the coast of Provence (160 km) and Italy (82 km), about 50 km from the island of Elba, only 12 km from Sardinia, and more than 450 km from North Africa and Spain. It is the smallest, but the most mountainous of the three Tyrrhenian islands and it has been inhabited by Man for at least 10,000 years. Faunistic and systematic data on ants of Corsica obtained in the last twenty years (Casevitz-Weulersse 1974, 1986a, b, 1990a, b) demonstrate the large diversity and wealth of the Corsican myrmecofauna, which is composed of 26 genera and 83 species. An ecological study of these 83 species and their distribution in the island had been presented in a previous paper (Casevitz-Weulersse 1990c). We present here the principal results of the biogeographical analysis of the Corsican ant fauna and compare it to neighboring countries.

GENERAL CHARACTERS OF THE CORSICAN MYRMECOFAUNA

Holldobler & Wilson (1990) list eleven and Bolton, more recently (1994), sixteen extant subfamilies in the family Formicidae. The four with the greatest worldwide distribution (Ponerinae, Myrmicinae, Dolichoderinae, Formicinae) are present in Corsica, together with a fifth subfamily (Leptanillinae) (Table 1).

Most Corsican species generally belong to the European Region and their distribution is either cosmopolitan (2.41%), holarctic (8.43%) or palaearctic (21.69%), or European (36.15%) only. The strictly Mediterranean species are less common (27.71%). Endemism is very low in the Corsican myrmecofauna; only three of the 83 species present on the island can be qualified as endemic today, with the caveat that endemism is a very relative and variable concept. For example, several species which had long been considered as strictly cyrno-sardinian were shown by enlarged faunistic surveys and taxonomic revisions to be much more widely distributed, e.g., *Leptanilla revelierei* Emery, *Messor wasmanni* Krausse, (Casevitz-Weulersse 1992) or *Epimyрма corsica* (Emery) (Buschinger & Winters 1985). Two of the three endemic Corsican species have been recently described: *Leptothorax melas* by Espadaler et al. (1984b) and *Stenamamma orousseti* by Casevitz-Weulersse (1990a); the third species, *Tetramorium* sp., is under study.

Table 1. Formicidae of Corsica: subfamilies, genera and number of species for each genus.

Sub-families (5)	Genera (26)	Number of species (83)
Leptanillinae	<i>Leptanilla</i>	1
Ponerinae	<i>Cryptopone</i>	1
	<i>Hypoponera</i>	2
Myrmicinae	<i>Ponera</i>	1
	<i>Smithistruma</i>	2
	<i>Epitritus</i>	1
	<i>Myrmica</i>	4
	<i>Stenammas</i>	2
	<i>Aphaenogaster</i>	4
	<i>Messor</i>	4
	<i>Pheidole</i>	1
	<i>Crematogaster</i>	1
	<i>Solenopsis</i>	2
	<i>Monomorium</i>	1
	<i>Myrmecina</i>	1
	<i>Leptothorax</i>	15
	<i>Epimyrmica</i>	3
	<i>Tetramorium</i>	7
Dolichoderinae	<i>Strongylognathus</i>	1
	<i>Tapinoma</i>	3
	<i>Bothriomyrmex</i>	1
	<i>Linepithema</i>	1
Formicinae	<i>Plagiolepis</i>	2
	<i>Lasius</i>	9
	<i>Camponotus</i>	7
	<i>Formica</i>	6

COMPARISON WITH OTHER REGIONS

French Mainland.—The island shares 69 of its 83 species with continental France, which includes 44 genera and about 180 species (Bernard 1968). However, 14 Corsican species, including *Aphaenogaster spinosa* Emery and *Messor minor* (André) which are among the most common ants on the island, are not found on mainland France. However, a dozen genera included in the mainland fauna are absent in Corsica. In particular, *Manica* (Myrmicinae), *Dolichoderus* (Dolichoderinae), *Cataglyphis*, *Proformica* and *Polyergus* (Formicinae) are probably really absent, because they are immediately noticed when they are present in a biotope. Other genera which have not been found on the island include parasitic and very rare species; it is possible that they will be discovered there in the future.

Other Mediterranean Regions.—The myrmecofaunas of fifteen Mediterranean regions where reliable faunistic surveys have been published in recent decades were compared to that of Corsica (Table 2). At the genus level, these regions have a high number of genera in common with Corsica.

At the species level, their degree of similarity with Corsica was estimated using the Jaccard's coefficient (JC) according to the following formula : $JC = (Cab \times 100) / (A + B - Cab)$, with Cab = number of species in common in regions A and B; A and B = total number of species in region A and region B. By con-

Table 2. Comparison between the myrmecofaunas of fifteen Mediterranean regions and Corsica (8720 km², 26 genera, 83 species).

Regions	Surface (km ²)	Total no. of genera (no. of genera common with Corsica)	Total no. of species (no. of species common with Corsica)	Jaccard's coefficient
Sardinia ¹	24,100	24 (24)	64 (52)	54.74
Provence ²	26,135	34 (25)	116 (60)	43.17
Tuscan Archipelago ³	1000	22 (21)	45 (35)	37.63
Liguria ⁴	5415	29 (24)	78 (42)	35.29
Mt Ventoux ⁵	?	21 (16)	63 (38)	35.19
Sicily ⁶	25,500	29 (23)	79 (41)	33.88
North of Spain ⁷	252,370	34 (25)	136 (54)	32.74
Latium ⁸	17,200	22 (19)	53 (33)	32.04
Tuscany ⁹	29,000	26 (21)	63 (35)	31.53
All of Spain ¹⁰	504,748	44 (26)	214 (63)	26.92
Yugoslavia ¹¹	225,800	38 (25)	161 (51)	26.42
Portugal ¹²	90,000	20 (17)	73 (30)	23.81
Baleoric Islands ¹³	4980	19 (19)	42 (24)	23.76
Greece ¹⁴	131,944	39 (25)	222 (46)	17.76
Algerian Forests ¹⁵	?	35 (23)	114 (24)	13.87

¹ Baroni-Urbani 1971, Casevitz-Weulersse 1974. ² Soyer 1951, Ovazza 1954, Bernard 1968, 1983, Gaspard 1968. ³ Baroni-Urbani 1971. ⁴ Baroni-Urbani 1971. ⁵ Du Merle 1978. ⁶ Baroni-Urbani 1971. ⁷ Collingwood 1978, Collingwood & Yarrow 1969, Espadaler 1979, 1980, 1981, 1986a, b, Espadaler & Collingwood 1982, Espadaler & Restrepo 1983, Espadaler & Riasol 1983, Espadaler & Roda 1984, Espadaler et al. 1984, Martinez-Ibanez & Espadaler Gelabert 1986, Tinaut 1985, 1987a, b, 1988. ⁸ Baroni-Urbani 1971. ⁹ Baroni-Urbani 1971. ¹⁰ (see 7). ¹¹ Agosti & Collingwood 1987. ¹² Collingwood 1978. ¹³ Collingwood & Yarrow 1969, Comin del Rio & De Haro Vera 1980, Comin del Rio & Espadaler Gelabert 1984. ¹⁴ Agosti & Collingwood 1987. ¹⁵ Cagniant 1968, 1973.

vention, A = number of species in Corsica (83) and B = total number of species in the country being compared (Table 2). The distribution of all the species included in the Corsican myrmecofauna and their presence in these 15 Mediterranean regions had been listed in a preceding paper (Casevitz-Weulersse 1992).

Note that Corsica (with an area of 8720 km²) has 83 species, but Sardinia (area 2.8 times larger) has only 64 species and Sicily has 79. Several large continental regions also have a smaller number of species in relation to their area when compared to Corsica. On contrast, Mount Ventoux, the Tuscan archipelago, and the Balearic islands have a diversified and rather rich myrmecofauna. These observations are partly due to a lack of faunistic surveys and taxonomic studies in many southern European countries.

In spite of missing or incomplete data, comparisons are still interesting. As expected, considering the palaeogeographical history of the Mediterranean region, Sardinia (JC: 54.74) has the highest biocoenotic similarity with Corsica, followed by Provence (JC: 43.17). Similarity with western Mediterranean regions, continental or insular, is very low (all of Spain, Balearic islands, Portugal), as it is for more distant regions (Greece and Algerian forests).

Table 3 indicates that 26 species of the Corsican myrmecofauna have a wide geographical distribution in the Mediterranean region. Most of them also have a large worldwide distribution. Only two species are strictly Mediterranean, the rest belong to the European, palaeartic, or holarctic domains.

Table 3. 26 Corsican species with a wide geographical range in 15 Mediterranean regions and their world distribution.

	Species	No. of Mediterranean regions inhabited	Absent from:	World distribution
1	<i>Ponera coarctata</i> (Latreille)	15		european
2	<i>Aphaenogaster subterranea</i> (Latreille)	13	Tuscany, Portugal	palaeartic
3	<i>Messor capitatus</i> (Latreille)	14	Greece	mediterranean
4	<i>Messor structor</i> (Latreille)	14	Algerian forests	european
5	<i>Pheidole pallidula</i> (Nylander)	15		palaeartic
6	<i>Crematogaster scutellaris</i> (Olivier)	15		european
7	<i>Solenopsis fugax</i> (Latreille)	12	Portugal, Balearic Islands, Algerian forests	palaeartic
8	<i>Myrmecina graminicola</i> (Latreille)	15		palaeartic
9	<i>Leptothorax nylanderi</i> (Förster)	13	Balearic Islands, Algerian forests	european
10	<i>Leptothorax recedens</i> (Nylander)	12	Tuscan Archipelago, Tuscany, Portugal	european
11	<i>Leptothorax tuberum</i> (Fab.)	12	Tuscany, Balearic Islands, Algerian forests	european
12	<i>Tetramorium caespitum</i> (L.)	14	Algerian forests	holoartic
13	<i>Tetramorium semilaeve</i> André	12	Liguria, Mt Ventoux, Algerian forests	palaeartic
14	<i>Tapinoma nigerrimum</i> (Nylander)	12	Mt Ventoux, Yugoslavia, Greece	mediterranean
15	<i>Plagiolepis pygmaea</i> (Latreille)	15	Algerian forests	european
16	<i>Lasius alienus</i> (Förster)	15		holoartic
17	<i>Lasius emarginatus</i> (Olivier)	13	Balearic Islands, Algerian forests	palaeartic
18	<i>Lasius flavus</i> (Fab.)	14	Balearic Islands	holoartic
19	<i>Lasius niger</i> (L.)	15		holoartic
20	<i>Camponotus aethiops</i> (Latreille)	12	Portugal, Balearic Islands, Algerian forests	palaeartic
21	<i>Camponotus lateralis</i> (Olivier)	15		palaeartic
22	<i>Camponotus piceus</i> (Leach)	14	Algerian forests	european
23	<i>Camponotus truncatus</i> (Spinola)	13	Latium, Portugal	palaeartic
24	<i>Camponotus vagus</i> (Scopoli)	13	Tuscany, Balearic Islands	european
25	<i>Formica cunicularia</i> Latreille	13	Balearic Islands, Algerian forests	european
26	<i>Formica fusca</i> (L.)	12	Tuscan Archipelago, Sicily, Balearic Islands	holoartic

As is the case for the Corsican populations, the myrmecofaunas of the entire Mediterranean region are primarily European.

To sum, Corsica has a diversified myrmecofauna with a rather high number of species, considering its area. However, this fauna is not original and it is constituted mostly of generalist, ubiquitous species with a wide distribution.

ORIGIN OF THE CORSICAN ANT POPULATIONS

Ants are social insects. Reproduction of their colonies and propagation of their species follow particular rules. The creation of new colonies and their implantation at a given location differ depending on the species and can occur from the aerial arrival of winged, impregnated females; along or in groups, from the movement of portions of colonies including one or several egg-laying wingless females and workers, or from the isolation of workers with larvae of future queens and males. In some cases, groups of isolated workers without brood (eggs, larvae, pupae) can also originate new colonies by various ways (inseminated workers or parthenogenesis). Species can reach an island either by active (flight of winged sexual individuals) or passive transportation. However, the queens of many ant species are unable to cover long distances by air, unless they are small enough to be carried by air currents.

As with ants, an European or a palaeartic component of the fauna is often demonstrated for other insects and invertebrates from Corsica. However, endemism rates vary considerably among the groups, depending on their age and mode of dispersal. For many groups, endemism is rather high and occurs at the species, or more often subspecies level but rarely at the generic level. Corsican populations of Coleoptera (Sainte-Claire Deville 1906/1914, 1926; Jeannel 1942, 1961a, b), Plecoptera, Trichoptera, blepharocerid Diptera (Giudicelli 1975, Cianficconi & Moretti 1990), Araneae (Canard 1989), Diplopoda (Mauries 1969) and terrestrial Oligochaeta (Omodeo 1961, Omodeo & Rota 1987) are largely composed of species which have evolved locally from a Tertiary fauna that found a refuge on the island, particularly on its high mountains.

The situation is different with the ants. The last link between Corsica and the continent seems to have occurred between 6 and 5 million years ago during the Messinian episode, and also during the early ice ages. Corsica has been a true island only in the last 100,000 years (Gauthier & Vigne 1987). When links existed with the continent, at the time of the early ice ages at the beginning of the Quaternary era, the myrmecofauna probably already included genera and species identical to those that can be observed today (Casevitz-Weulersse 1992). The intermittent indirect links between Corsica and continental Europe at the time of the first ice ages allowed, on several occasions, the passage of various species which were already modern. If the low endemism seen here is true, it would demonstrate that there has been almost no local ant evolution.

Recent studies in Corsica and Sardinia on vertebrate, particularly mammalian faunas, have shown that the current situation is essentially due to voluntary and involuntary human action (Vigne & Alcover 1985). All present day taxa in Corsica were absent before the Holocene (Vigne 1987, 1992) and their endemism is low, at the level of a few subspecies. In the same manner as the mammals, it is quite possible that ant populations were constituted in part from species introduced

by Man to this island, which was one of the first to be colonized in the Mediterranean.

Finally, it should be noted that our conclusions on the Mediterranean Basin myrmecofauna are very close to those of Blondel (1982, 1984) concerning the biogeographical origin of avifaunas. Blondel observed the same European aspect of the populations and low endemism in birds nesting in Corsica and in the rest of the Mediterranean region that is also observed in ants.

The introduction of ants in Corsica probably occurred before the final separation of the island from the continent. The paleogeographical history of the island and the paleontology of the Formicidae explain why this distribution of subfamilies is similar to that of most temperate countries (Casevitz-Weulersse 1992). However, the present composition of this fauna can also be explained by taking into account the early arrival of Man, whose essential role in the modern composition of the Corsican faunas we are only now beginning to understand.

In addition to human exchanges between the island and the continent during the post-Pliocene, several factors came into play for the creation of the myrmecofauna as we can observe it today. As emphasized by Bernard (1968) and Lamotte (1986), chance plays a large role in the installation of diverse species on an island. The early comers occupy all the habitats and leave no room for others.

The lack of success in Corsica of a species as conquering as *Linepithema humile*, the "Argentine ant" (Casevitz-Weulersse 1986b, 1992) and the cohabitation in the same biotope of several species on the same genus, which seem to exploit the same food sources, e.g., *Messor wasmanni*, *M. minor*, and *M. capitatus* on backshores (Casevitz-Weulersse 1990c) or *Lasius niger* and *L. emarginatus* in citrus orchards (Casevitz-Weulersse 1993) are a few of many examples that demonstrate competition and association phenomena. They will have to be analyzed in detail if we want to understand how the ant populations in Corsica were constituted and how they operate.

Competition, intrinsic capacity of species to occupy new territories, high colonizing power are characteristics which have allowed certain species to become established at the expense of others. The particular diversity of Corsican environments has certainly also contributed to the persistence or the implantation of widely varied species. All of these factors have contributed in the present characteristics of ant populations in Corsica.

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